

SURVIVAL AND HABITAT OF RUFFED GROUSE NESTS IN NORTHERN MICHIGAN

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ABSTRACT.—Effective management of Ruffed Grouse (*Bonasa umbellus*) populations requires a full understanding of chick production. Previous reports of nest survival for Ruffed Grouse are biased because they did not account for successful nests being more likely to be found, and the role of habitat quality in determining nest survival is unknown. We determined survival rates of Ruffed Grouse nests in northern lower Michigan using the less biased Mayfield estimator, defined differences between first and second nests, and compared the local habitat characteristics of successful and unsuccessful nests. Median hatching dates were 10 June for first nests ($n = 34$) and 1 July for second nests ($n = 6$). First nests had a lower survival rate (0.442, 95% CI = 0.270–0.716), a higher mean clutch size (12.7 eggs \pm 0.3 SE), and higher egg hatching rate (0.960, 95% CI = 0.900–0.997) than did second nests (nest survival = 0.788, 95% CI = 0.491–1.00; clutch size = 7.3 eggs \pm 0.3 SE; and hatching rate = 0.826, 95% CI = 0.718–0.925). Nest survival, annual production (3.4 hatchling females/adult female, 95% CI = 2.3–5.0), and fall recruitment (1.0 juvenile females/adult female, 95% CI = 0.3–2.4) were less than previously reported estimates. Habitat characteristics at nest sites varied widely and did not differ appreciably between successful and unsuccessful nests. Received 16 July 2002, accepted 22 February 2003.

Although the importance of nest success to understanding grouse population fluctuations has been recognized (Gullion 1970), it remains little studied. Brander (1967), Barrett (1970), and Maxson (1974, 1978a) studied the behavior of female grouse during the breeding season, and information about hatching dates and clutch size has come from many sources (Hale and Wendt 1951, Cringan 1970, Rusch and Keith 1971, Porath and Vohs 1972, Kubisiak 1978, Maxson 1978b, Small et al. 1996). A full understanding of grouse chick production, however, is lacking because little information is available for nest survival rates, renesting attempts, and nesting habitat.

Survival rates of Ruffed Grouse (*Bonasa umbellus*) nests, some based on large samples (Bump et al. 1947), have been reported only as the percentage of observed nests that hatched chicks (Rusch and Keith 1971, Maxson 1978b, Small et al. 1996). This apparent survival rate contains substantial positive bias because successful nests are more likely to be

located by researchers (Mayfield 1961, Johnson 1994). The degree of bias may not be constant among studies, so comparing apparent survival rates among different areas or time periods may not be appropriate. Accurate quantitative estimates of nest survival are necessary for comprehensive evaluation of population vital rates (i.e., survival and reproductive success rates) and demographic simulation modeling.

Annual fertility (i.e., hatchling females/adult female; Johnson 1994) is only partially dependent upon nest survival. An accurate estimate of fertility also depends upon clutch size and the rates at which females attempt multiple nests within a single breeding season (Caughley 1977). The second nesting attempt of a marked female grouse after failure of the first nest was first documented by Barrett (1970). The only additional data for known second nests were reported by Small et al. (1996). The assumption of renesting often is based on evidence of a secondary peak in hatching that usually involves notably smaller clutches (Cringan 1970, Porath and Vohs 1972, Maxson 1978b). The survival rate of second nests may be different from first nests because most second nests are at risk later in the spring, when environmental conditions such as weather and predation pressure may be different.

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The significance of habitat quality to chick production needs further study (Martin 1995). Bump et al. (1947), Gullion (1977), Maxson (1978b), and Thompson et al. (1987) have described nest sites, but few have related their findings to nest survival rates. Also, no one previously has quantified the amount of cover at nest sites. Our objectives were to determine nest survival rates, to define differences between first and second nests, and to compare the habitat characteristics of successful and unsuccessful nests.

METHODS

Study area.—We conducted our study in the northern portion of the lower peninsula of Michigan. Study sites were located in the Huron National Forest (HNF; 44° 32' N, 83° 58' W) and Pigeon River Country State Forest (PRCSF; 45° 11' N, 84° 26' W). Each covered approximately 200 km² and was selected because it was perceived to contain high quality Ruffed Grouse habitat. The HNF site was dominated by stands of aspen (*Populus* spp.), mixed hardwoods (e.g., *Acer* spp.), and oaks (*Quercus* spp.). The PRCSF site was approximately 100 km to the north of the HNF site and was similar but had fewer stands of oaks and more stands of conifers (*Pinus resinosa*, *P. strobus*, *Thuja occidentalis*). Detailed information about the forest structure, overstory vegetation, and Ruffed Grouse habitat at both sites is in Gormley (1996). A weather station 19 km northwest of the HNF site recorded the following conditions. April 1996: precipitation sum = 7.5 cm, mean daily low temperature = -3.2° C, mean daily high temperature = 8.6° C; May 1996: precipitation sum = 3.6 cm, mean daily low temperature = 2.5° C, mean daily high temperature = 17.0° C; April 1997: precipitation sum = 1.9 cm, mean daily low temperature = -2.4° C, mean daily high temperature = 11.4° C; and May 1997: precipitation sum = 5.9 cm, mean daily low temperature = 2.4° C, mean daily high temperature = 14.1° C (Midwestern Climate Center, Champaign, Illinois, unpubl. data).

Chick production.—We located nests during spring, 1996 and 1997, by monitoring female grouse that had been captured and marked with a radio transmitter the previous fall (see Clark 1996). We approached females if radio tracking indicated that they were in the same

location on two consecutive days. Once nests were found, we monitored them every 1–5 days, considering them active if radio tracking indicated that the female was on the nest. We approached nests for visual inspection only to determine final clutch size and when the female was not at the nest. Within two days after a nesting attempt was complete, we counted the number of eggs that did, and did not, hatch, marking an attempt as successful if ≥ 1 egg hatched. We monitored unsuccessful females to locate renesting attempts and observed second nests using methods identical to those for first nests. All procedures for capturing, handling, and marking grouse were reviewed and approved by the Michigan State Univ. All-University Committee on Animal Use and Care (AUF# 10/93–400–03).

We estimated clutch initiation dates from the earliest known point in the nesting sequence. If we found a nest during the egg-laying period, we subtracted 1.3 days for each egg from the earliest date during which we observed an incomplete clutch (Maxson 1974). If we found a nest during incubation, the clutch initiation date could be determined only if the nest was successful. In this case we subtracted from the hatching date 1.3 days to lay each egg in the full clutch and a 25-day incubation period beginning with the last egg.

Habitat characteristics.—We obtained the age and dominant overstory vegetation type of forest stands containing marked grouse nests from the U.S. Forest Service and the PRCSF headquarters. After the nesting attempt was complete and the female was no longer occupying the nest, we analyzed characteristics of each nest site. We sampled nesting habitat at the HNF site on 11–15 June 1996 and 11 June to 3 July 1997. We sampled at the PRCSF site on 7 July 1996 and 7 August 1997. We noted the direction and distance between nests and any solid objects within 1 m. We recorded aspect of the ground slope as one of eight general compass directions. We counted live woody stems ≥ 1 m tall in a 10 × 10-m plot centered on the nest. We quantified cover at the nest site as estimates of percent visual obstruction of a 1-m-tall profile board from 5 m and 15 m in front of the nest, a 1 × 1-m ground cover plot centered on the nest, and a spherical densiometer view of can-

opy cover above the nest (Higgins et al. 1994). We also measured the distances from the nest to the nearest opening (no live woody stems and no canopy cover for 5 m in one straight line dimension), mature aspen tree (≥ 15 cm dbh), and conifer tree (≥ 1 m tall). A more detailed description of field methods is in Larson (1998).

Data analysis.—We used the Mayfield (1961) method to calculate nest survival rates and the methods of Johnson (1979) to calculate the SE of survival rates and of differences in survival among categories. When >1 day elapsed between the last two nest checks, we used the midpoint as the date of nest success or failure. To evaluate potential underestimation of variance in survival rates (Ford et al. 2001), we simulated and analyzed 10,000 bootstrap samples of our empirical data (Efron and Tibshirani 1993). We also simulated 10,000 bootstrap samples to construct confidence intervals (CIs) on egg hatching rates and used nests as the sampling unit rather than eggs. We estimated chick production and fall recruitment for the population by multiplying the CIs (Moore 1979) of clutch size, nest survival, egg hatching rate, and chick survival from a concurrent study (approximately 0.302 ± 0.091 SE; Larson et al. 2001).

Due to the descriptive nature of our study and relatively small sample sizes, we avoided statistical hypothesis testing and modeling (e.g., logistic regression) in favor of estimating the magnitude and precision of important differences. We searched for differences in chick production variables (e.g., clutch initiation date, clutch size, survival rate) and habitat characteristics of nest sites between levels of variables such as age of the female, nesting attempt, and nest fate. Most of our data were not normally distributed, so we based our calculation of estimated differences and CIs (exclusive of nest survival) on statistics associated with Wilcoxon's rank sum (Hollander and Wolfe 1973:75–79). We often present CIs or ranges rather than SD or SE because the latter do not represent the asymmetrical nature of uncertainty around many of our estimates.

RESULTS

Chick production.—We observed 41 nesting attempts by 34 female grouse. Six of the 35 first nesting attempts were made by three

females observed both years, and four were made by females subsequently observed making a second nesting attempt during the same year. We observed two additional second nests made by females whose first nests we did not locate. Of the other 25 observed first nests, we excluded one from all survival analyses (but included it in the estimation of habitat characteristics) because it was found after it had been destroyed by a predator, one from all habitat analyses (including survival estimated by habitat categories) because we did not sample habitat at that nest site, and two others from estimation of habitat characteristics because they were abandoned when the female was killed away from the nest.

The date of clutch initiation ranged from 26 April to 4 June. The median date for first nests ($n = 27$) was 1 May. Nesting appeared to begin approximately four days earlier in 1997 than in 1996 (95% CI = 0–7 days). Of the five second-year (SY) females that survived the destruction of their first nest, only two made a second attempt at nesting. All four of the after-second-year (ASY) females in the same situation, however, made a second nesting attempt. Two females that attempted second nests had been incubating for 9 and 13 days, respectively, when their first nest was destroyed. The date of first nest destruction for females that subsequently attempted a second nest was as late as 28 May. Second clutches were initiated 3–6 days after the destruction of the first nest. The median date of second clutch initiation was 29 May ($n = 6$).

Nests hatched between 4 June and 3 July. The median was 10 June for first nests ($n = 23$) and 1 July for second nests ($n = 5$). Three first nests had known incubation times of 24, 25, and 27 days for clutches of 13, 13, and 14 eggs, respectively. Two second nests had known incubation times of 21 and 26 days for clutches of eight and seven eggs, respectively.

The mean full clutch size was 12.7 eggs ± 0.3 SE for 30 first nests and 7.3 eggs ± 0.3 SE for 6 second nests. Mean clutch size was smaller for SY females than for ASY females for first (a difference of 0.2 eggs ± 0.6 SE) and especially second nests (a difference of 1.3 eggs ± 0.5 SE). All eggs hatched in 83% of the 23 successful first nests and 20% of the 5 successful second nests. Mean hatching rates were 0.960 (95% CI = 0.900 – 0.997) and

TABLE 1. Characteristics of Ruffed Grouse nests observed in northern Michigan during 1996 and 1997.

Characteristic	<i>n</i>	Mean ± SE or median (5th–95th percentiles)
DSR ^a	40	0.9832 ± 0.0048
DSR during 1996	12	0.9814 ± 0.0092 (0.9809 ± 0.0091) ^b
DSR during 1997	28	0.9840 ± 0.0056 (0.9835 ± 0.0060)
DSR of first nests	34	0.9807 ± 0.0058 (0.9804 ± 0.0059)
DSR of second nests	6	0.9930 ± 0.0070 (0.9928 ± 0.0073)
DSR of SY females ^c	20	0.9797 ± 0.0076
DSR of ASY females ^c	19	0.9885 ± 0.0057
DSR during egg laying	11 ^d	0.9524 ± 0.0465
DSR during incubation	36 ^d	0.9895 ± 0.0040
Diameter of nest object (cm) ^e	34	10 (2–30)
Horizontal cover (%) ^f from 5 m	38	45 (10–85)
Horizontal cover (%) ^f from 15 m	38	85 (25–100)
Ground cover (%) ^f	38	53 (15–85)
Canopy cover (%) ^f	38	90 (59–99)
Distance to opening (m) ^g	38	14 (2–224)
Distance to aspen (m) ^g	38	12 (0–165)
Distance to conifer (m) ^g	38	2 (0–240)

^a DSR = daily survival rate of nests.

^b Estimates in parentheses are from 10,000 bootstrap samples.

^c SY = second-year; ASY = after-second-year.

^d Number of nests known to be in the nesting stage during ≥1 of the days it was under observation (i.e., some nests represented both stages). One nest failed during 21 days of observation of nests known to be in the egg laying stage, and seven nests failed during 663.5 days of observation of nests known to be in the incubation stage.

^e Diameter of the tree, snag, stump, log, or branch against or under which the nest was built.

^f Percent visual obstruction of a 1-m-tall profile board (horizontal cover), of bare ground from a 1.5-m height (ground cover), or above 1.5 m estimated using a spherical densiometer (canopy cover).

^g Distance from the nest to the nearest opening with no live woody stems or canopy cover for ≥5 m in one straight-line dimension, live aspen tree ≥15 cm dbh, or live conifer tree ≥1 m tall.

0.826 (95% CI = 0.718–0.925) for successful first and second nests, respectively.

We observed nests for 714 nest-days (median = 20 days/nest). Twenty-eight nests were successful, 10 were destroyed by predators, and two were abandoned when the female was killed while away from the nest. The mean daily survival rate was 0.9832 ± 0.0048 for all nests. Our sample of first nests surviving to hatch were at risk a mean of 40.1 days, and second nests were at risk for 32.6 days. Using the same daily survival rates and standard nest durations of 42 and 34 days, however, survival rates for the entire nesting interval were 0.491 (95% CI = 0.327–0.733) for first nests and 0.562 (95% CI = 0.405–0.777) for second nests. Our data do not support differences in daily survival rates by nest stage, nesting attempt, year, age of female, or any categorical habitat characteristics of nest sites (Table 1). The SE of daily survival rate in bootstrap samples indicated almost no bias in our original estimates of precision (Table 1).

First nests produced a mean of 6.0 (95% CI = 3.8–9.3) hatchlings per female (nest surviv-

al × clutch size × egg hatch rate = $0.491 \times 12.7 \times 0.96$). Second nests produced a mean of 3.4 (95% CI = 2.2–5.1) hatchlings per female ($0.562 \times 7.3 \times 0.83$). Only 6 of 13 females with a destroyed first nest, however, made a second nesting attempt, and they represented approximately 23% of the population of females that began the breeding season ($[1 - 0.491] \times 0.46$). Therefore, a mean of 6.8 (95% CI = 4.5–10.0) hatchlings were produced per female present in the spring population ($6.0 + [0.23 \times 3.4]$). Survival of those hatchlings was approximately 0.302 (Larson et al. 2001), so recruitment into the fall population was 2.1 (95% CI = 0.6–4.8) juveniles per spring female.

Habitat characteristics.—Overall, forest stands containing marked grouse nests were a median of 32 (5th–95th percentiles range = 13–81, *n* = 28) years old with a median of 6,050 (5th–95th percentiles = 2,000–24,400, *n* = 38) woody stems/ha. Equal numbers (13 each) of Ruffed Grouse nests were located in aspen and conifer overstory vegetation categories, but fewer nests were in other decidu-

ous types ($n = 9$). One nest was at the edge of a grassy opening and four were located on private property where overstory vegetation types were not defined. All females ($n = 40$) positioned their nests against one of five objects: a live tree (62.5%), a snag (12.5%), a log (12.5%), a branch laying on the ground (7.5%), or a stump (5.0%). Seven live nest trees were aspens, 10 were other deciduous species, and 8 were conifers. Second nests were positioned against larger objects (median = 25 cm in diameter, $n = 5$) than were first nests (median = 10 cm, $n = 31$; median difference = 15 cm, 95% CI = 5–23 cm). Nests were found in similar proportions on all sides of objects. Although 23 nests were located on level ground, 14 of 17 nests on slopes had at least some southern or eastern exposure. We found no other appreciable differences in nesting habitat between successful and destroyed nests, first and second nests, or the nests of SY and ASY females (i.e., the CI on differences included zero).

DISCUSSION

Chick production.—Ruffed Grouse clutch initiation and hatching dates are thought to be highly dependent upon latitude, with the nesting season beginning earlier in the more southern portions of its range (Maxson 1978b). Working in three areas of Michigan within 100 km of the HNF and PRCSF sites, Fisher (1939) reported a mean hatching date of 9 June, excluding one nest that hatched on 8 July. These dates and those reported by Maxson (1978b; 4–8 June) for a similar latitude in Minnesota closely matched the hatching dates of first and second nests we observed. Our estimates of hatching dates were approximately 1–2 weeks later than those found at lower latitudes (Bump et al. 1947:284, Cringan 1970, Porath and Vohs 1972, Kubisiak 1978). Porath and Vohs (1972) reported a peak in the hatching of second nests three weeks after the peak for first nests in southern Ontario. The difference between the median hatching dates of first and second nests in our study was exactly 21 days, which suggests that the timing of second nests relative to first nests may be consistent regardless of latitude. The possible earlier nesting during 1997 may be attributable to the warmer, drier weather during the month of April that year.

It has been considered unlikely that female grouse would attempt a second nest if they had begun incubation of their first nest before it was destroyed by a predator (Bump et al. 1947:291). Two females in our study renested after incubating their first nest for 1–2 weeks, and five renesting hens in Wisconsin incubated first nests for 5–18 days (Small et al. 1996). Stage of the nesting sequence, therefore, may not be as important to the probability of re-nesting as previously thought (Bump et al. 1947:291). Although renesting may be more likely to occur for extremely early first nest failures (e.g., early May) than for extremely late failures (e.g., early to mid-June), we have presented evidence that the age of the female may affect the likelihood of renesting during mid- to late May.

Our estimate of first nest clutch size is greater than the means of 11.5 and 11.9 eggs in “early nests” found in other studies (Bump et al. 1947:361, Cringan 1970) and the means of 10.6–12.5 eggs reported by those who did not distinguish between first and second nests (Leopold 1933:362, Fisher 1939, Fallis and Hope 1950, Rusch and Keith 1971, Maxson 1978b). Our estimate of clutch size for second nests is less than the means of 7.5 and 8.5 eggs in “late nests” reported by Bump et al. (1947:361) and Cringan (1970), respectively. The differences between the results for clutch size from this study and others may be due to the lack of, or imprecise, classification of first and second nests during earlier studies. Clutch size for known first nests in Wisconsin (11.0), however, also was less than in our study, whereas clutch sizes of known second nests were similar (7.4 versus 7.3 in our study; Small et al. 1996).

In New York, Bump et al. (1947:365) observed that the rate of egg hatching in successful “late nests” was approximately 2% less than in “earlier nests.” The same was observed by Small et al. (1996), but their rates were much lower (about 0.44). We found a larger decrease in the egg hatching rate in second nests (12.6%).

Bump et al. (1947:359–360) suggested that SY females may produce smaller clutches than ASY females. Their conclusion was based on captive grouse and one wild female with clutches of 10, 13, and 12 eggs when she was one, two, and five years old, respectively.

Maxson (1978b), however, reported no difference in clutch size between SY and ASY females. Our results agree with those of Bump et al. (1947:359–360) and Small et al. (1996), and suggest that perhaps the variability in clutch size among females prevents the detection of a difference in clutch size according to age that is apparent within individual females.

Estimates of apparent nest survival for Ruffed Grouse range from 0.46 to 0.86 (Bump et al. 1947:312, Rusch and Keith 1971, Maxson 1978b, Small et al. 1996). Because most nests are not located until after incubation begins, including those of radio-tagged females, one cannot account for the significant, but unknown, number of nests that are destroyed during the egg-laying period with the apparent survival method. Although our Mayfield nest survival estimate for second nests (0.79) falls within the range of apparent nest survival rates, our Mayfield survival estimate for first nests (0.44) is substantially below most previous estimates. Chick production, therefore, is likely less than previously reported. This has implications for the relative importance of reproduction and fall-to-spring survival in the fluctuations of Ruffed Grouse populations. Given that both nest and chick survival (Larson et al. 2001) may be less than previously expected, concern about recruitment of new individuals into the fall population may increase.

Habitat characteristics.—Our sample of Ruffed Grouse nests was too small for us to detect differences in habitat characteristics between successful and destroyed nests because of the high variability in the vegetation data. Nearly all dominant overstory vegetation types were used. Less than 5% of nests in studies by Bump et al. (1947:127–128) and Maxson (1978b) were located in conifer cover types, but more than a third of the nests in our study were located in conifer stands. The age of a forest stand also appears to be less important than the actual cover it provides. Gullion (1977) reported that aspen stands between 25 and 30 years old provide preferred nesting habitat because stem densities are <4,900 stems/ha and the closed canopy prevents the growth of dense understory vegetation, which supposedly aids the incubating female in detecting predators. By comparison, none of the 13 aspen stands that contained nests during

our study were 25–30 years old; nine were younger, four older. The females in our study nested in forest stands of nearly all seral stages, which is consistent with the results of Bump et al. (1947:127–128).

Although stem density results from a study of Ruffed Grouse nest sites in an oak-hickory (*Carya* spp.) forest (Thompson et al. 1987) agree with Gullion's (1977) prediction of preferred nesting cover in areas with low stem densities, fewer than half of the nest sites in our study were in areas of <4,900 stems/ha. This probably is due to the definition of a stem that was used. Stem density measurements that include only relatively large stems (e.g., >2–3 cm dbh) are better descriptors of the quality of grouse nesting habitat because they indicate the degree of forest thinning to which Gullion (1977) was referring. On the other hand, using a less restrictive definition (e.g., woody stems >1 m tall), as we did following a definition by Cade and Sousa (1985), seems to provide a redundant measure of understory cover.

We were unable to find previous studies quantifying the amount of cover around Ruffed Grouse nest sites, and only Bump et al. (1947:128) gave a qualitative description. Apparent nest survival during their study was not affected by the density of undergrowth. Maxson (1978a), however, found higher apparent nest survival in mixed hardwoods, where a thick covering of ferns emerged during the incubation period, than in oak stands, where it did not. The amount of cover, quantified by several visual obstruction methods, did not appear to affect nest survival during our study. Bracken ferns (*Pteridium aquilinum aquilinum*) were not present when females selected their nest sites, but they provided much of the horizontal cover and ground cover at most nest sites subsequent to the nesting season and presumably during the later stages of incubation.

The proximity of grouse nests to a forest opening is thought to be significant for brood habitat immediately after chicks hatch (Maxson 1978a, Kimmel and Samuel 1984), not necessarily for nesting habitat. The distances to the nearest opening in our study are remarkably similar to the results from two other studies. Nearly 50% of all nests were within 10 m of an opening (Maxson 1978b), and

75% were within 30 m (Bump et al. 1947: 132–134). As expected, none of these studies revealed any association of distance to the nearest opening with nest survival. Distances from nests to the nearest mature aspen tree, the buds and leaves of which are important winter and early spring foods for Ruffed Grouse, also were similar between our study and others (Schladweiler 1968, Maxson 1978a).

Conclusions.—Our study suggests that survival of Ruffed Grouse nests is less than previously estimated. This may be a factor in declining grouse populations and the slow recovery of populations from low periods during the 10-year cycle observed in the northern part of their range. Increasing survival of first nests will have a much larger impact on grouse populations than a similar increase in survival of second nests due to differences in clutch size and egg hatching rates. Our study also outlines the wide range of habitat characteristics that may be successfully utilized by nesting Ruffed Grouse.

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